1. Quaternary History of the Mediterranean Vegetation of Chile

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The climate of the mediterranean region of Chile in a wide sense (30° to 39° S) is determined principally by the Southern Pacific Subtropical Anticyclone (SPSA). This system has an average center at around 30° S and presents a conspicuous annual cycle of latitudinal displacement. The winter rains in the *mediterranean* zone of Chile are associated with the northern position of the anticyclone during its annual cycle. This placement favors frontal activity associated with the westerly wind belt in the middle latitudes. During summer, displacement of the anticyclone to the south, and contraction in the same direction of the westerly wind belt, produces the dry season in the mediterranean region of Chile (Aceituno 1990).

To the north of 30° S, arid conditions are observed throughout the year as a result of the permanent influence of the Pacific Anticyclone, the desiccating action of the Peruvian cold ocean current, and the rain-shadow effect of the Andes on moisture-laden winds from the east. Only the far northern Andes receive summer rains (100 to 300 mm) of tropical origin (Arroyo et al. 1988; Grosjean et al. 1991). South of 39° S, rains of western origin are received through most of the year, although the mediterranean tendency is still found with one or two dry months, as far south as 42° S in inland areas (di Castri and Hajek 1976).

Climatic anomalies appear in central Chile (to the north of 35° S) that have been related to global phenomena of atmospheric circulation, such as the Southern Oscillation (SO). During the negative phase of the SO, associated with El Niño events (ENSO events), atmospheric pressure is unusually low in the SPSA domain. This situation has been associated with a tendency toward warmer and more humid winters in central Chile (Aceituno 1990).

Corresponding with the transitional character of these two contrasting climatic systems, the vegetation of the mediterranean region of Chile is characterized by conspicuous floristic and physiognomic heterogeneity. In this chapter, the Quaternary history of the mediterranean vegetation is discussed, based on the palynological record. Emphasis is given to the influence of paleoenvironmental changes and climatic fluctuations of the last glacial–interglacial cycle. The present geographic distribution of forest species of central–south Chile is interpreted in relation to the dynamics of paleoenvironmental change documented in the palynological record.

Vegetation Formations

A succession of xeric to mesic vegetation formations occurs in the mediterranean region of Chile along the latitudinal gradient. This sequence accords with an increase in rainfall from north to south. Semiarid formations, xerophytic matorral, and "savannas" with *Acacia caven* and *Prosopis chilensis* in the northern mediterranean sector are succeeded in turn by subtropical broad-leaved forest and matorral formations (sclerophyllous forests) in the central sector, and by deciduous forests of *Nothofagus* farther south. The latter gradually intergrade into temperate evergreen rain forests in the Lake region (Fig. 1.1).

The rain-shadow effects exerted by the two mountain ranges also determine strong east–west variation in the vegetation. At 35° S, sclerophyllous formations are restricted to the Coast range and the Andean foothills, and *Acacia caven* woodland and semiarid matorral predominate in the central depression. South of 35° S, deciduous *Nothofagus* forest occurs in the central depression and on the eastern slopes of the Coast range, and different types of evergreen forests are distributed on the western slopes.

Vestigial communities are found discontinuously on mountain summits and gullies of the Coast range (Fig. 1.2). These include olivillo (*Aextoxicon punctatum*) cloud forests at 30°30′ S, palm stands of *Jubaea chilensis*, isolated populations of deciduous *Nothofagus obliqua* in central Chile, coniferous forests with *Araucaria araucana* and *Fitzroya cupressoides*, and the Magellanic moorlands in the south-central region. An elevated number of endemic and monotypic taxa show narrow and discontinuous distribution ranges in the Coast range in central-south Chile. Examples of strongly endemic genera are *Pitavia*, *Valdivia*, *Jubaea*, *Gomortega*, *Tetilla*, *Lardizabala*, and *Latua*.

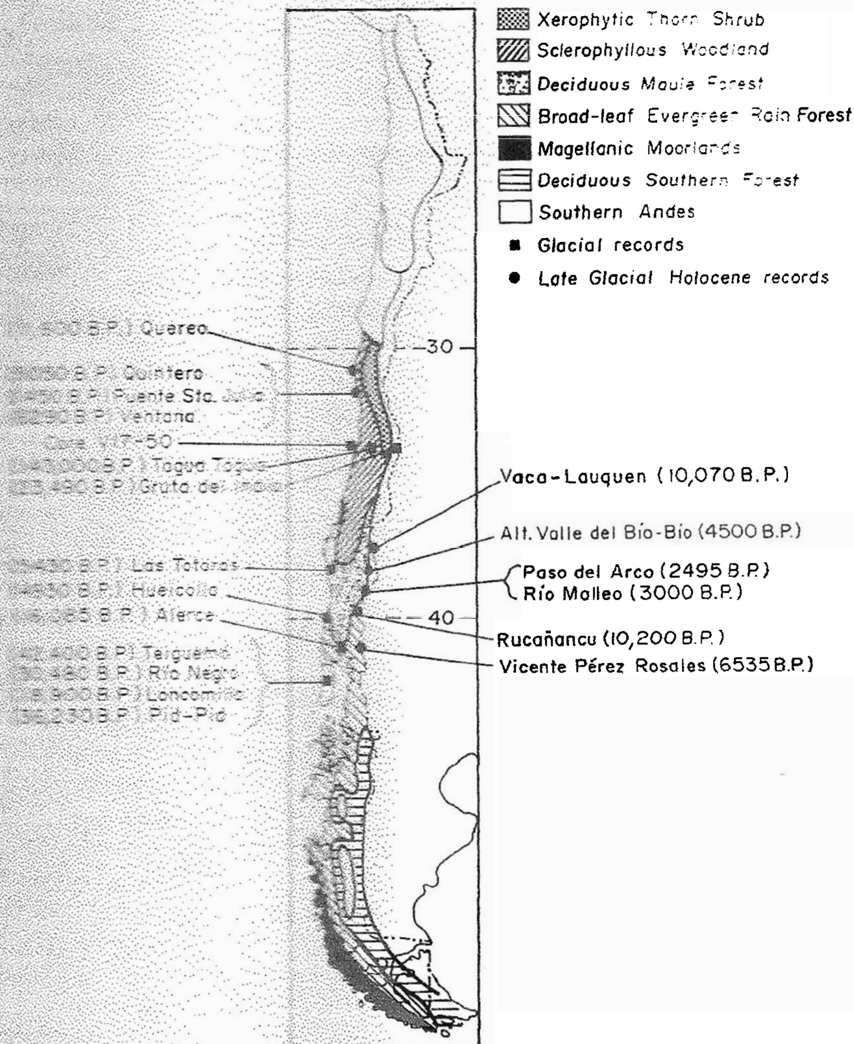

Figure 1.1. Vegetation formations in the mediterranean and southern temperate zone in Chile (Schmithüsen 1956). Palynological records mentioned in text denoted by circles.

Glacial History of Mediterranean Vegetation

Evidence from the temperate Andes in South America shows that during the Quaternary various glacier advances affected practically all the territory to the south of 42°30′ S, the central depression in the Lake region (39° to 42° S), and the Andean slopes to the north of 39° S (Fig. 1.1). During the last glaciation, the maximum temperature depression (6° to 7° C colder) and glacier

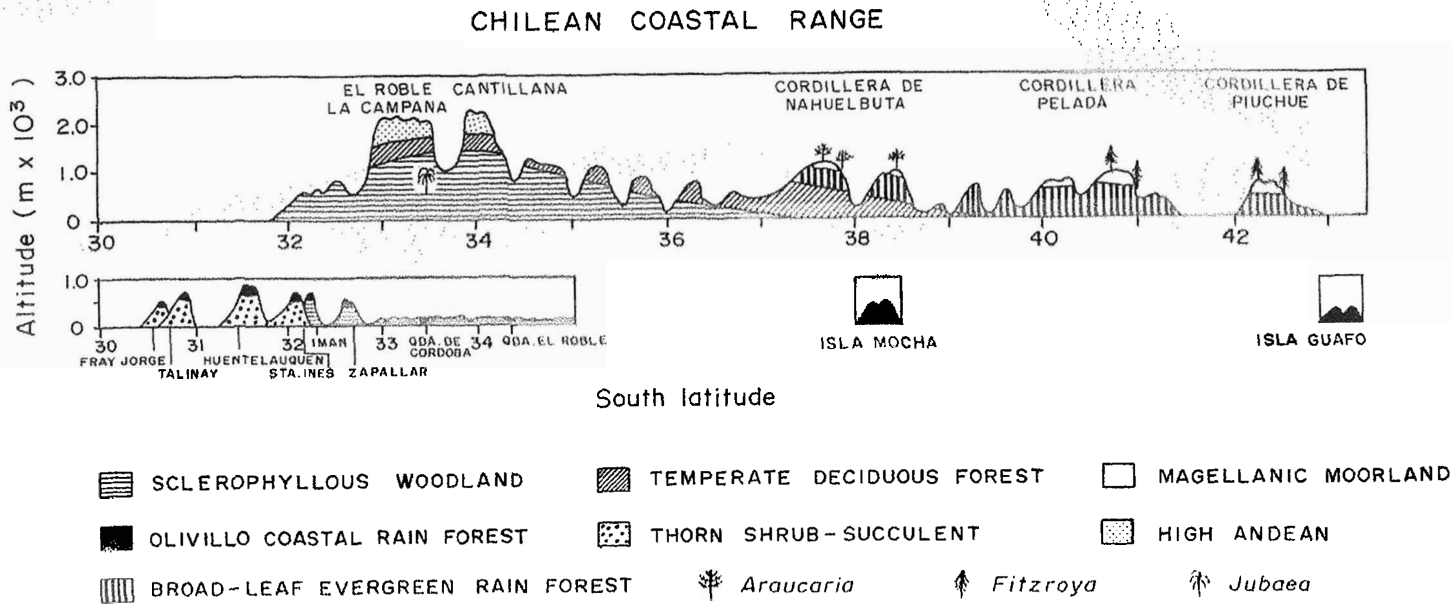

Figure 1.2. Altitudinal profile of the Coast range in central and south-central Chile, showing discontinuous distribution of relictual communities.

advances occurred between 20,000 and 18,000 years B.P., and were in phase with the Northern Hemisphere (Mercer 1976; 1984; Porter 1981; Clapperton 1990; 1991; Denton, unpublished data). A second glacier advance, between 15,000 and 14,500 years B.P., preceded rapid deglaciation that succeeded immediately and without interruption. Unequivocal reversions corresponding to the oscillation of the Younger Dryas period of the Northern Hemisphere have not been registered.

Geomorphologic and paleopedologic investigations (Garleff and Schäbitz 1993; Veit 1993) show that areas lacking morphodynamic activity in the Upper Quaternary were reduced to south of 40° S because of the glacial advance, fluvioglacial processes in the plains of the central depression, and intense vulcanism. These authors have established preliminary altitudinal limits of influence of periglacial processes for the Coast range during the Upper Pleistocene, such as solifluction, indicative of scarce vegetational cover. The inferior altitudinal limit of these processes extends from 1500 m in La Campana (32°55′ S) to 600 m in the Nahuelbuta Range (37°49′ S). This limit is at 300 m in the Sarao Range (40°57′ S), and reaches the base of the Piuchué Range (42°30′ S) farther south (Garleff and Schäbitz 1993).

Palynological Records

The documented glacial history of the vegetation is very scarce for the mediterranean region in Chile. It is restricted to three records at the same latitude (Fig. 1.1). A record for ocean sediments near the coast of Valparaíso (Core V17-50, 34°30′ S, 71°10′ W; Groot and Groot 1966) indicates that the glacial ages were characterized by forests dominated by the hygrophyllous conifer *Podocarpus*, while more diverse broad-leaved forests predominated during the interglacials. The Tagua Tagua record (34°30′ S, 71°10′ W; Heusser 1990a) shows that during the last glacial maximum (25,000 to 14,000 years B.P.) the vegetation in the central depression comprised conifers and *Nothofagus* for trees, Gramineae, Compositae, and Chenopodiaceae for herbs, and aquatic taxa. East of the Andes in the precordillera in Argentina, the record for Gruta del Indio (34°45′ S, 68°22′ W; D'Antoni 1983) indicates glacial vegetation dominated by Gramineae that has been interpreted as a northern extension of the Patagonian steppe.

Palynological evidence from temperate latitudes with mediterranean tendencies (Fig. 1.1), between 39° and 42° S (Heusser 1966; 1984a; 1990b; Villagrán 1985; 1988; 1990), show a glacial vegetation that was dominated by an open forest of *Nothofagus*, conifers, *Drimys*, and Myrtaceae. Cold-temperate taxa from more austral formations such as the Magellanic moorland elements (e.g., *Astelia*, *Dacrydium*) are recorded during the last glacial maximum.

Abundance of subantarctic, cold-temperate elements such as *Nothofagus*, *Prumnopitys*, *Podocarpus*, *Dacrydium*, and *Astelia* in the present mediterranean region of south-central Chile (34° S to 42° S), along with high lake levels, abundant austral molluscs, microalgae, and other aquatic taxa recorded in Laguna Tagua Tagua in central Chile (Covacevich 1971; Varela 1976; Heusser 1990a) suggest rainy, glacial conditions.

On the island of Chiloé, dominance by conifer and *Nothofagus* trees, mixed with a mosaic of Magellanic moorland species, suggests that the glacial vegetation would have been equivalent to that found today discontinuously distributed on the mountain summits of the Coast range between 39° and 43° S. In the central depression of south-central Chile, the singular combination of Gramineae and Compositae pertaining to open communities, and of trees such as conifers and *Nothofagus*, suggest a physiognomically homogeneous parklike glacial landscape without an equivalent in the present Chilean vegetation. This condition was perhaps comparable to the forest–steppe ecotone on the eastern Andean slopes today. This glacial vegetation is concordant with an abundant megafauna that became extinct at the begin-

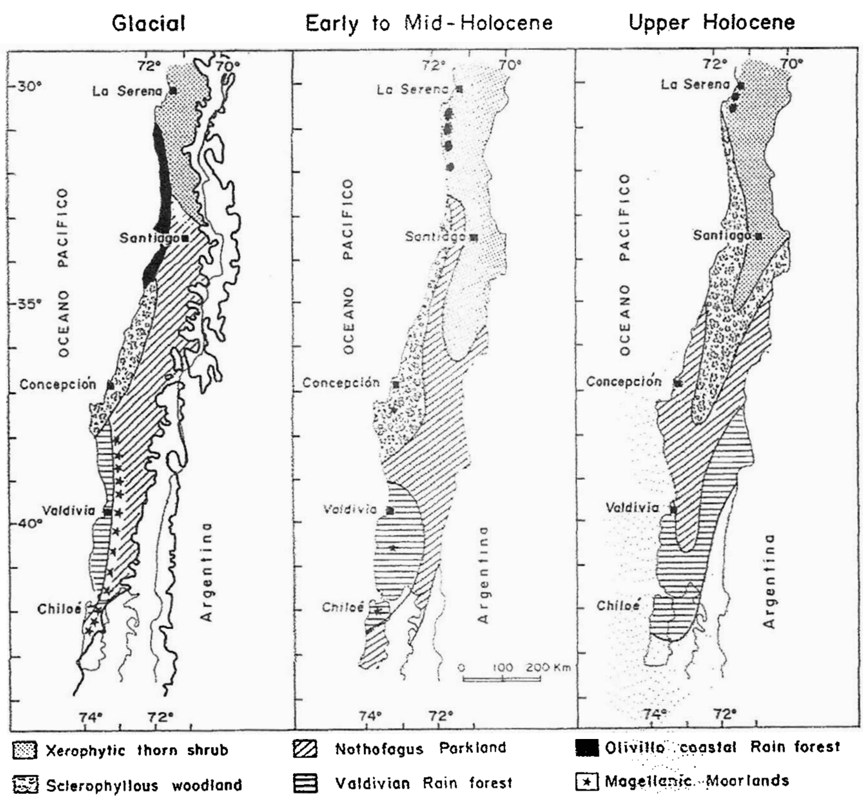

Figure 1.3. Reconstruction of Glacial, Lower to Middle Holocene, and Upper Holocene vegetation, in accordance with the paleoenvironmental record.

ning of the Holocene (Nuñez et al. 1983). Such glacial vegetation would have occupied the central depression, replacing the present closed-canopy broadleaved forests that succeed from north to south along the latitudinal gradient. Indicators belonging to the sclerophyllous, deciduous mediterranean and Valdivian forests are lacking. The Coast range, between 35° and 42° S, is proposed as a refugium for such forests during the glacial period (Fig. 1.3).

Reconstruction of the Last Glacial Maximum Climate

According to oceanic temperature reconstructions for the last glacial maximum (CLIMAP 1981), at 18,000 years B.P., oceanic circulation was characterized by: displacement toward the equator and areal contraction of subpolar waters; more pronounced thermal gradients in temperate regions; relatively stable positions for the central gyres in the oceans of the Southern Hemisphere; a rise in divergence and upwelling; and a thermal equator near or slightly deviated north from its present position. These changes suggest an intensification of oceanic, and also probably atmospheric, circulation during the last glacial maximum.

The meridional temperature gradient determines the intensity of the anticyclone and of the westerly wind belt and thus the vigor of the atmospheric circulation (Harrison et al. 1983). Analyzing ocean temperatures from seven cores shows that between 44° and 50° S, the temperature gradient was strongest 18,000 years ago, enabling the intensification (Markgraf et al. 1992) and northern expansion of the westerly wind belt, as proposed by various authors (Heusser 1984a; 1990a; 1990b; Villagrán 1988; 1990; Caviedes 1990). This expansion would explain the presence of glacial records of a cold-temperate subantarctic element to the north of its present geographic distribution, as at low-altitude sites on the island of Chiloé, and of *Nothofagus* and coniferous forests in the central depression in south-central Chile to 34°30′ S.

The pronounced vegetational contrast documented in the glacial records at 34°30′ S, with a grassy steppe to the east of the Andes, a park–steppe ecotone in the central depression of Chile, and a hygrophyllous podocarp forest on the coast, suggest reinforcement of the orographic effects of the Andes and the Coast range, and an even stronger east–west vegetation gradient than is present today. This scenario is consistent with more intense westerlies and greater elevation of the Andes and Coast ranges, reaching 5800 m and 2333 m, between 30° and 35° S, compared with 3400 m and 1533 m, respectively, to the south of 35° S and with more pronounced continental conditions recorded to the south of 32° S on the eastern side of the Andes (Garleff et al. 1991), and would explain the relictual cloud forests in coastal ravines and mountains of north-central Chile that were probably more continuous during the ice ages (Fig. 1.3).

From 27° to 33° S, glacial, periglacial, lacustrine, and pedologic evidence (Veit 1991a; 1991b) indicates colder and drier conditions during the last glacial maximum, with strong morphodynamic activity. The only stable zones were at the altitude of thermal inversions that cause littoral fogs (Veit 1993). There is also now evidence in the northern Andes (24° S) of an arid climate during the glacial maximum, without glacier formation and low lake levels (Grosjean et al. 1991). The present distributions of altiplanic, desert, and mediterranean elements in the high-elevation flora also suggest that desert barriers could have been more pronounced during part of the Pleistocene (Arroyo et al. 1982; Villagrán et al. 1983).

Vigorous anticyclones in the South Pacific and South Atlantic oceans, in positions equivalent to the present winter extremes (Villagrán 1993a) would determine the strong increment in aridity documented in the record in the north of Chile, and the relatively constant position of the center of the arid diagonal during the Upper Quaternary as proposed by Garleff et al. (1991). Considering the stronger atmospheric circulation during the glacial maximum and increased upwelling of cold waters north of 30° S, this scenario is not incompatible with intensified westerlies, but rather implies compression of the present mediterranean climate zone and, in consequence, sharper contrast between the hygrophyllous vegetation in the south and semiarid vegetation in the north.

Late-Glacial Vegetation and Climate

Paleotemperature curves in the Late-Glacial from the Antarctic show a marked tendency toward a rise in temperature from 15,000 B.P., reaching an optimum ca. 10,000 years B.P. Radiocarbon-controlled glacial chronology indicates that deglaciation was rapid and uninterrupted in the Lake region of southern Chile (Mercer 1984), at least from 13,000 years B.P.

The palynological (Villagrán 1991) and fossil-beetle (Ashworth and Hoganson 1987) records from the Lake region show evidence for rapid recolonization of North Patagonian rain forest, beginning 14,000 to 13,000 years B.P. The same arboreal taxa (*Podocarpus*, *Fitzroya*, *Drimys*, Myrtaceae, and *Nothofagus*), present in traces during the glacial maximum, expand and Magellanic moorland species disappear from low-elevation sites. The Valdivian rain-forest species, dominant here today, are still recorded only in traces during the Late-Glacial.

In central Chile the Tagua Tagua record (Heusser 1990a) shows that glacial vegetation persisted in the central depression (34°30′ S) up to 10,000 B.P. In the more northern littoral Quereo (32° S) record, a very diverse semiarid matorral for the Late-Glacial (Villagrán and Varela 1990) with strong representation of aquatic and palustrine taxa suggest humid conditions. The sclerophyllous forest species, today dominant in central Chile, have not yet been recorded; however, many of these species are insect pollinated (Moldenke 1977) and might not accumulate great quantities in the pollen record. The vegetation suggests that humid climate covered a wider geographic area during the Late-Glacial as temperature began to rise.

Geomorphological and soil-development studies carried out in north-central Chile by Veit (1991a; 1991b; 1993) between 27° and 33° S, show that cold and dry phases of the glacial maximum, characterized by strong morphodynamic activity, were succeeded by cold and wet phases in the Late-Glacial (16,000 to 10,000 years B.P.), with development of soils on the coast and in the interior, along with glacial advances in the Andes. Similar climatic conditions prevailed in the northern Chilean Andes (Grosjean et al. 1991) during this time.

This paleoclimate scenario, with glacial advances and a rise in rainfall of eastern origin in the northern Chilean Andes and the Altiplano; glacial advances in the Andes of north-central Chile, with development of paleosoils of temperate–humid climates on the coast and in the interior; and deglaciation in south-central Chile, would be plausible if the Late-Glacial is conceived as a slow relaxation of the glacial mode of circulation, gradual warming of the oceans, and weakening of Atlantic and Pacific anticyclones. The glacier advance, with doubled rainfall of eastern origin in the Altiplano (Kessler 1985), suggests that the Atlantic Convergence Belt was displaced to the south of its current position during the Late-Glacial (Kessler 1991; Villagrán 1993a).

Holocene Vegetational History

Records from central Chile (32° to 35° S) (Fig. 1.4), indicate an abrupt change in the vegetation in the Pleistocene–Holocene transition around 10,000 years ago. Aquatic taxa disappeared and the number of palustrine species, Gramineae, and arboreal traces decreased at Quereo, with a rise in dominance of Compositae and Umbelliferae (Villagrán and Varela 1990). Glacial forest elements disappeared and were substituted for by herbs, mainly Chenopodiaceae/Amaranthaceae in Tagua Tagua (Heusser 1990a). At Gruta del Indio, the steppe glacial vegetation was replaced by allochthonous taxa (D'Antoni 1983). These vegetational changes are consistent with a change from cold-wet to warm-dry conditions during the Pleistocene–Holocene transition.

Evidence from geomorphological and soil studies (Veit 1991a; 1991b; 1993) between 27° and 33° S, shows that during the Holocene there were fluctuating cold-humid and warm-dry phases on the coast of north-central Chile (Fig. 1.4, column 1). The cold-humid phases were accompanied by development of soils and greater snow accumulation in the high mountains; in contrast, the interior climate was dry during all of the Holocene.

The humid versus dry phases of the Early and Middle Holocene, respectively, established by Veit, correspond with equivalent phases in Tagua Tagua (Fig. 1.4, column 4) that were characterized by dominance of Gramineae versus Chenopodiaceae, respectively (Heusser 1990a). Both phases also correspond to fluctuations in the Tagua Tagua lake levels (Varela 1976), with

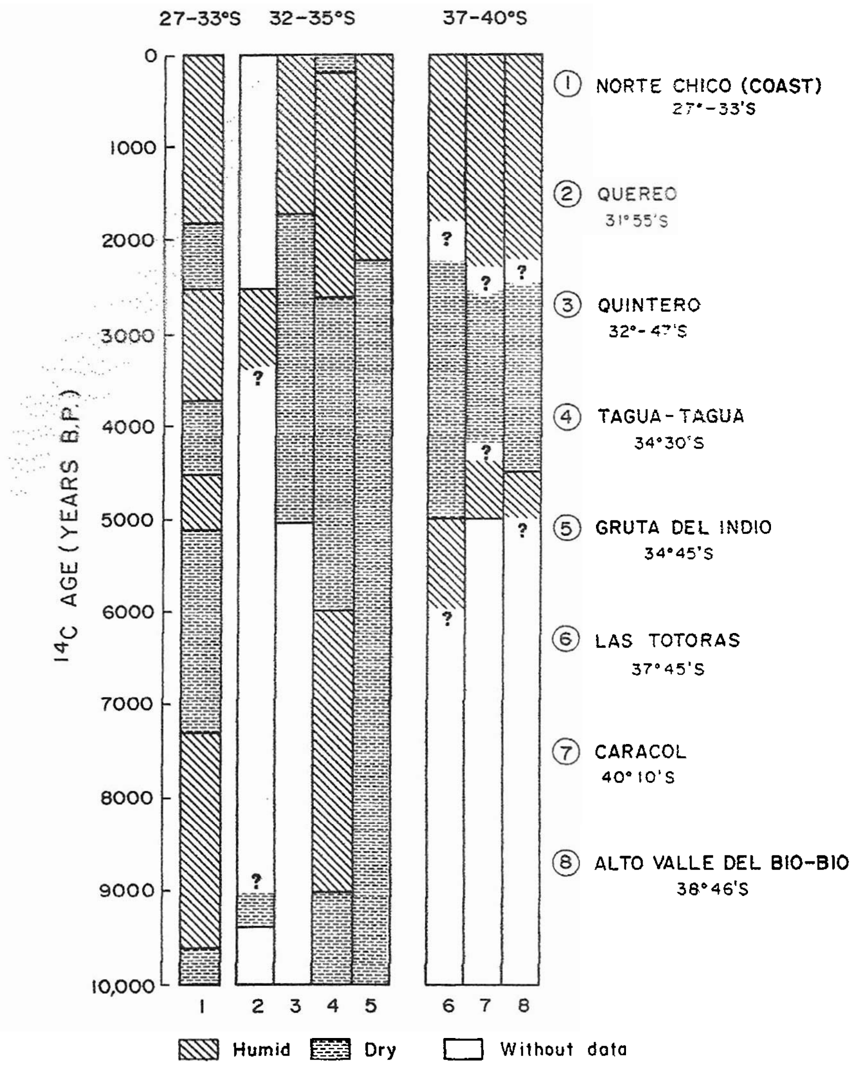

Figure 1.4. Chronological sequence of the humid and dry phases during the last 10,000 years, in accordance with the palynological records discussed in the text and geomorphological-pedological studies by Veit (1993) in north-central Chile.

relatively high levels in the Early Holocene and desiccation in the Middle Holocene.

All the mediterranean-zone records (Quintero, Ventana, and Puente Santa Julia; Fig. 1.1) show that after 5,000 (4,500) B.P. (Fig. 1.4, column 3) an arid phase was followed at around 2,500 years B.P. by a humid phase, with forests and swamps developing on the coast of central Chile (Villagrán 1993b).

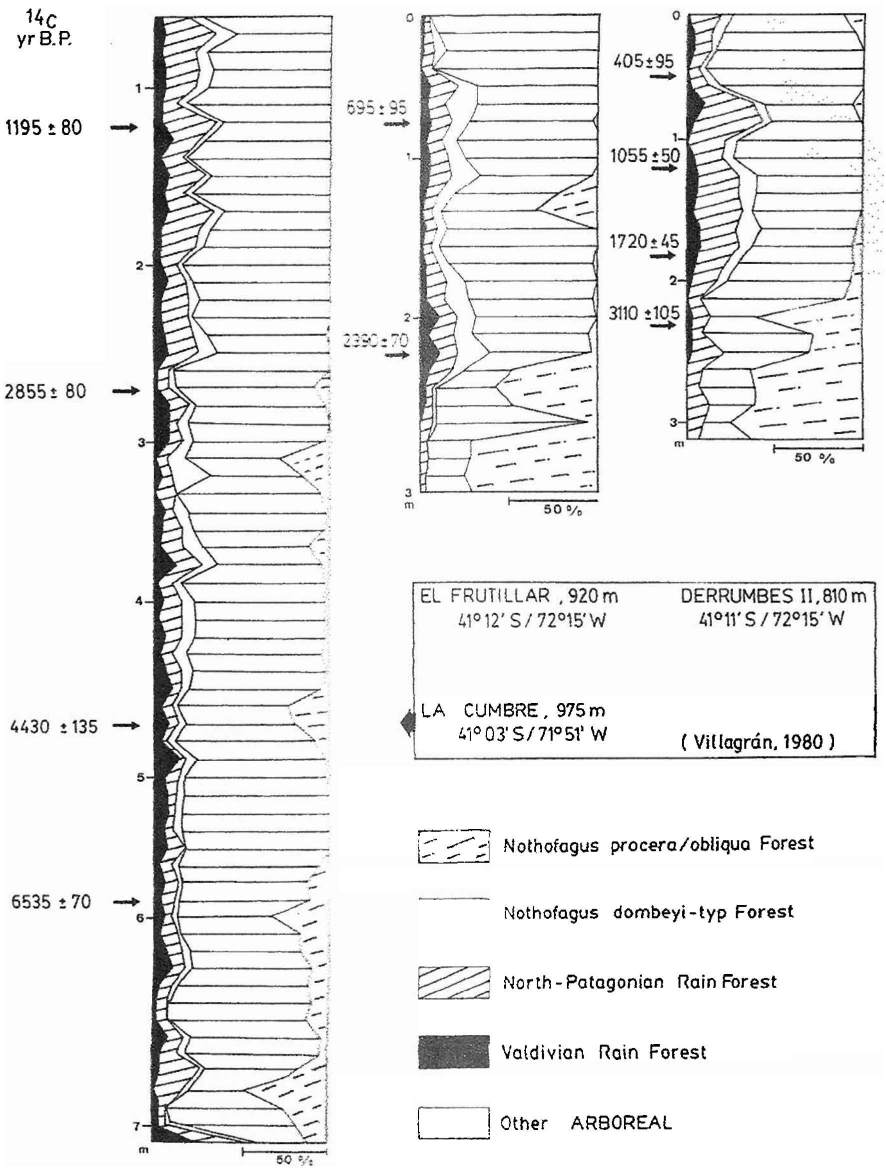

Figure 1.5. Composite diagrams of three records in the Andes from the Lake region that document expansion of deciduous forest element (*Nothofagus procera/obliqua*) during the Middle Holocene. (Adapted from Villagrán 1980.)

The records on the southern border of the mediterranean region in Chile (Fig. 1.4, columns 6 to 8), between 37° and 40° S, show an expansion of cold-temperate forests toward higher sites before 5,000 (4,500) years B.P. seen as *Araucaria* and *Nothofagus dombeyi* forests in the high Bio Bio valley (Rondanelli 1992), and forests with *Nothofagus dombeyi* and *Prumnopitys andina* and Magellanic moorland on the summit of the Nahuelbuta Range at Las Totoras, with expansion of the more thermophyllous forest with Proteaceae and Myrtaceae at El Caracol (Villagrán 1993b). Conversely, the records in the Argentinian Andes, as for Vaca Lauquén at 36°50′ S (Markgraf 1987), Paso del Arco at 38°50′ S, and Río Malleo at 39°36′ S (Heusser 1988), show arid conditions during a large part of the Holocene.

In the Lake region, from the beginning of the Holocene, we see rapid expansion of the more thermophyllous Valdivian rain-forest element (*Eucryphia*/*Caldcluvia* and *Weinmannia*), and restriction of the Late-Glacial *Nothofagus* type *dombeyi* and conifer forest toward both mountain ranges (Villagrán 1991). During the Early to Middle Holocene the deciduous-forest element (*Nothofagus* type *procera*/*obliqua*) occupied a dominant position more to the south of its present range, as documented by records at Rucañancu, 39°33′ S (Heusser 1984b) and Parque Vicente Pérez Rosales, 41° S (Fig. 1.5) (Villagrán 1980).

Holocene Climate Reconstruction

The glacial evidence already discussed indicates that in the Southern Hemisphere, glacial retreat at high latitudes immediately followed the last glacial advance (15,000 to 14,500 years B.P.); high oceanic temperatures were reached at 11,000 years B.P., with a maximum at 9,400 years B.P., in this way preceding by around 3000 years the maximum in the Northern Hemisphere (Harrison et al. 1983). This asymmetry between the maximum temperatures in the two hemispheres would have facilitated southern displacement of the Pacific Intertropical Convergence Belt during the Early Holocene (Villagrán 1993a). In this way, in the South Pacific during the Early Holocene, ocean temperatures would have been sufficiently high to cause a weakening of the oceanic circulation and a descent in atmospheric pressures in the area influenced by the SPSA. These conditions are analogous to those associated with present ENSO events.

Veit (1991a; 1991b) proposes a major event of very strong precipitation for the coast of north-central Chile between 9600 and 7300 years ago, corresponding to the higher accumulation of snow, higher alluvial cone activity, and intensification of erosion processes in the Andes. These conditions suggest a higher intensity and recurrence of ENSO events during this time. Even though this humid phase is detected in the palynological and lacustrine record of Tagua Tagua in central Chile, during this phase the dominant sclerophyllous forest of today does not appear, and only herbs are recorded. This situation suggests that this humid phase could correspond to a series of more frequent and intense ENSO events than seen today. Such conditions would have favored expansion of flora adapted to episodic rains as seen in the semiarid region today. At the same time these conditions would have restricted the expansion of taxa adapted to more regular seasonal rains, as for many woody mediterranean and cool-temperate forest elements in Chile (Fig. 1.3).

During the Middle Holocene, the relatively drier phases documented in all records from south-central Chile suggest that at this time the SPSA was probably more vigorous and in a more southerly position than today. Again these dry phases seem to have especially affected the northern area of the present mediterranean zone, because forest formation was absent at that time. Present climate and vegetation conditions would have been established during the Upper Holocene (Fig. 1.3).

Biogeographic Effects

Figure 1.6 shows variation in the percentage of forest species throughout Chile by degree of latitude (a total of 178 taxa were considered, including woody species, vines, and flowering plant epiphytes). Maximum richness occurs in a narrow latitudinal band between Maule and Valdivia (36° to 40° S) toward the southern end of the present mediterranean zone in Chile. Between 66% and 77% of species are concentrated in this band, but in sectors immediately to the north and south, only 33% (30° to 35° S) and 40% (40° to 46° S) of the species are seen, respectively.

This same pattern is repeated when we consider groups of woody taxa pertaining to the subantarctic cold-temperate element (e.g., *Nothofagus* and conifers) and the neotropical element requiring warmer temperatures (e.g., Flacourtiaceae and Myrtaceae), separately (Fig. 1.7). If we consider only the endemic species in these groups, the geographical area in which these taxa are concentrated is even more restricted (Fig. 1.7).

This pattern can be related to these events and processes:

1. Glacial advances that have directly affected the development of vegetation in all the territory south of 42° S, the central valley and the Andes in the Lake region (39° to 42° S) and the Andes in central Chile (33° to 39° S).
2. Periglacial processes such as glaciofluvial activity that affected a large part of nonglaciated sectors on the island of Chiloé, and the central depression in the Lake region.
3. Decrease in temperature (6° to 7° C) during the ice ages directly affecting the distributions of taxa and reducing habitats. Processes such as solifluction influenced high sectors (over 1500 m) of the northern Coast range to the base of this same mountain range in Chiloé.

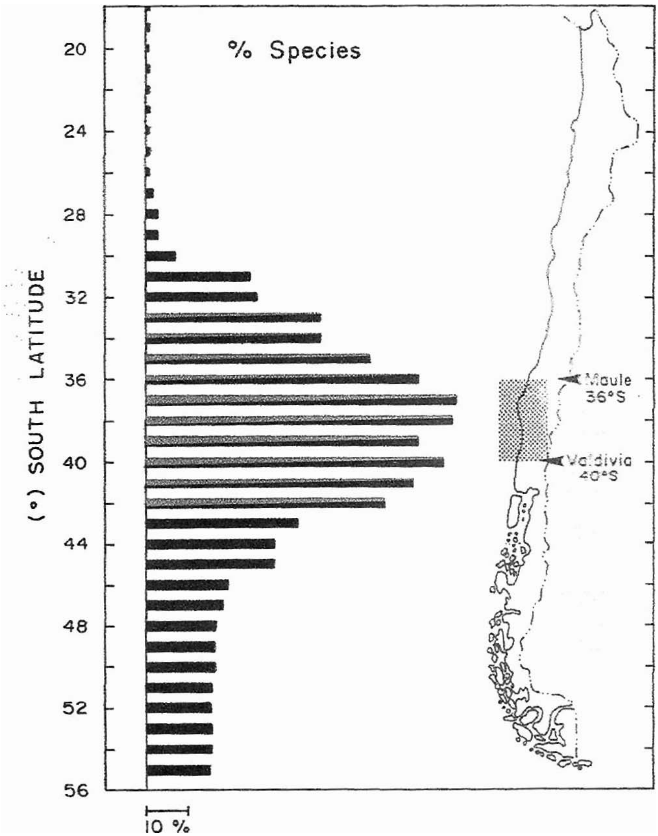

Figure 1.6. Latitudinal variation in the percentage presence of 178 forest species throughout Chile.

4. Change in the rainfall regime was probably the most critical factor for vegetation during glaciation. The intensification and northern expansion of the westerly wind belt, together with more vigorous anticyclones in the South Atlantic and South Pacific and higher upwelling intensity to the north of 30° S, would have provoked a more pronounced rainfall gradient throughout central-south Chile, with consequent compaction of the mediterranean zone.
5. The higher Andes and Coast ranges, to the north of 35° S, together with more vigorous atmospheric circulation, would have reinforced the rain-shadow effect exerted by these mountains, and accentuated the east–west rainfall gradient, provoking marked longitudinal zonation of the vegetation.
6. The interglacials would have been distinguished by unstable oceanic and atmospheric conditions, with maximum temperatures in the Early Holo-

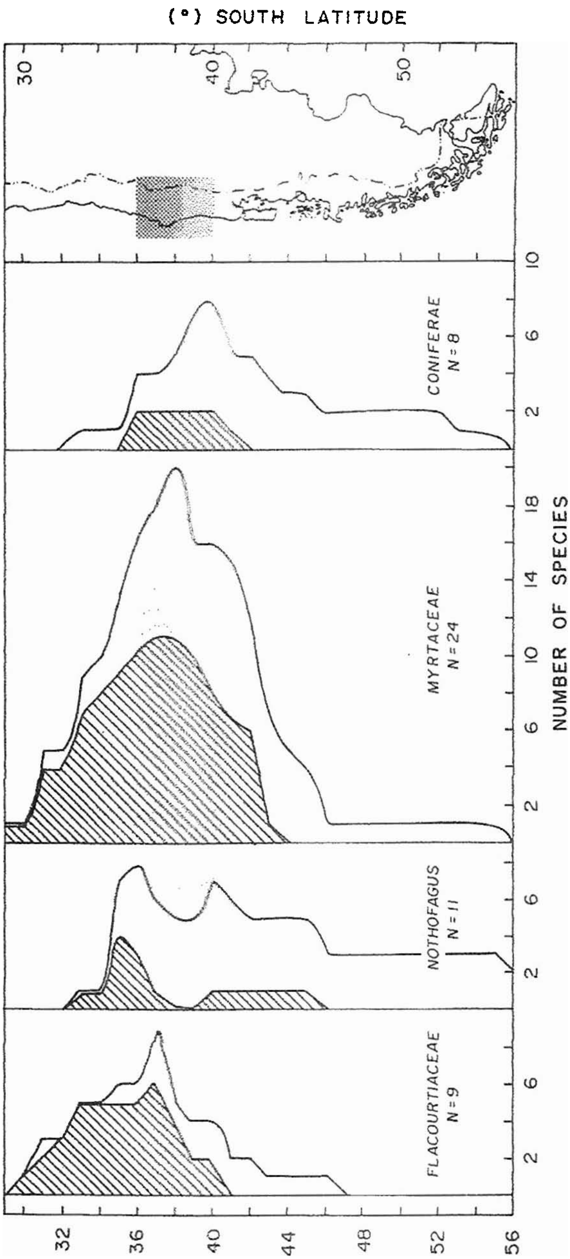

Figure 1.7. Latitudinal variation in number of woody forest species pertaining to Flacourtiaceae, Fagaceae, Myrtaceae, and conifers. Distribution of Chilean endemic species for these families denoted by shading.

cene and glacial readvances during the Late Holocene. The alternating humid and dry phases would have fundamentally affected distribution of species on the northern border of the present mediterranean region, especially to the north of 35° S. It is possible that these phases corresponded to periods of higher climatic oscillation, similar to those associated today with the negative and positive phases respectively of the Southern Oscillation.

Conclusions

Because of its transitional character between the arid and semiarid matorral vegetation in the north, and the temperate rainforest zone in the south, the vegetation in the mediterranean region of Chile (30° to 39° S) experienced profound and repetitive changes during the glacial–interglacial cycles in the Quaternary.

Glacial advances, periglacial effects, and climatic change have particularly affected the northern area in the actual mediterranean zone (30° to 35° S) and the greater part of the temperate zone to the south of 40° S. Stabler climatic conditions prevailed toward the southern end of the actual mediterranean zone, especially on the Coast range, which had better development of soils and more extensive vegetation cover. These stable conditions permitted maintenance of the Chilean forest flora there during the glacial periods. That the area with the highest concentration of species and endemism is between the Maule river and Valdivia (36° to 40° S) is an expression of this condition.

The repetitive climatic fluctuations of lesser scale during the Holocene (10,000 years B.P. to the present) have principally affected distribution of the subtropical element of the sclerophyllous forests in central Chile, which is more adapted to climatic conditions with regular winter rains. The humid postglacial phases registered in central Chile (to the north of 35° S) and in the Norte Chico, probably associated with more frequent and intense ENSO events, have favored expansion and differentiation of semiarid matorral adapted to episodic conditions of precipitation.

Acknowledgments

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